Original Articles

Application of a multi-disciplinary approach to reveal population structure and Southern Ocean feeding grounds of humpback whales

Leena Riekkola[a], Alexandre N. Zerbini[b,c], Olive Andrews[d], Virginia Andrews-Goff[e], C. Scott Baker[f], David Chandler[g], Simon Childerhouse[h], Phillip Clapham[b], Remi Dodémont[i], David Donnelly[j], Ari Friedlaender[f,1], Ramon Gallego[a,2], Claire Garrigue[k,i], Yulia Ivashchenko[b], Simon Jarman[l,m], Rebecca Lindsay[a], Logan Pallin[f,1], Jooke Robbins[n], Debbie Steel[f], James Tremlett[a,3], Silje Vindenes[a], Rochelle Constantine[a,o,*]

[a] School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand
[b] Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA
[c] Cascadia Research Collective, 218 1/2 W 4th Ave., Olympia, WA 98501, USA
[d] Conservation International (New Zealand & Pacific Islands), University of Auckland, Private Bag 92019, Auckland, New Zealand
[e] Australian Marine Mammal Centre, Australian Antarctic Division, 203 Channel Hwy, Kingston, TAS 7050, Australia
[f] Marine Mammal Institute, Hatfield Marine Science Center, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365, USA
[g] Australian Genome Research Facility, 6 Verdun St, Nedlands, Perth, WA 6009, Australia
[h] Blue Planet Marine, PO Box 3639, Richmond, Nelson, New Zealand
[i] Opération Cétacés, BP 12827, 98802 Nouméa, New Caledonia
[j] Killer Whales Australia, 8 Campbell Pde, Box Hill South, Victoria 3128, Australia
[k] UMR Entropie (IRD, Université de La Réunion, CNRS), Laboratoire d'Excellence-CORAIL, BPA5, 98848 Nouméa Cedex, New Caledonia
[l] Trace and Environmental DNA (TrEnD) Laboratory, Department of Environment and Agriculture, Curtin University, WA 6102, Australia
[m] CSIRO Indian Ocean Marine Research Centre, 39 Fairway – Level 4, The University of Western Australia, WA 6009, Australia
[n] Centre for Coastal Studies, 5 Holway Avenue, Provincetown, MA 02657, USA
[o] Institute of Marine Science, University of Auckland, Private Bag 92019, Auckland, New Zealand

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ABSTRACT

Obtaining direct measurements to characterise ecosystem function can be hindered by remote or inaccessible regions. Next-generation satellite tags that inform increasingly sophisticated movement models, and the miniaturisation of animal-borne loggers, have enabled the use of animals as tools to collect habitat data in remote environments, such as the Southern Ocean. Research on the distribution, habitat use and recovery of Oceania's humpback whales (*Megaptera novaeangliae*) has been constrained by the inaccessibility to their Antarctic feeding grounds and the limitations of technology. In this multi-disciplinary study, we combine innovative analytical tools to comprehensively assess the distribution and population structure of this marine predator throughout their entire migratory range. We used genotype and photo-identification matches and conducted a genetic mixed-stock analysis to identify the breeding ground origins of humpback whales migrating past the Kermadec Islands, New Zealand. Satellite tracking data and a state-space model were then used to identify the migratory paths and behaviour of 18 whales, and to reveal their Antarctic feeding ground destinations. Additionally, we conducted progesterone assays and epigenetic aging to determine the pregnancy rate and age-profile of the population. Humpback whales passing the Kermadec Islands did not assign to a single breeding ground origin, but instead came from a range of breeding grounds spanning ~3500 km of ocean. Sampled whales ranged from calves to adults of up to 67 years of age, and a pregnancy rate of 57% was estimated from 30 adult females. The whales migrated to the Southern Ocean (straight-line distances of up to 7000 km) and spanned ~4500 km across their Antarctic feeding grounds. All fully tracked females with a dependent calf (n = 4) migrated to the Ross Sea region, while 70% of adults without calves (n = 7) travelled further east to the Amundsen and Bellingshausen Seas region. By combining multiple research and analytical tools we obtained a comprehensive understanding of this wide-ranging, remote population of whales. Our results indicate a population recovering from exploitation,

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* Corresponding author at: School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand.
  E-mail address: r.constantine@auckland.ac.nz (R. Constantine).
[1] Institute of Marine Sciences, University of California – Santa Cruz, 115 McAllister Way, Santa Cruz, CA 95060, USA.
[2] School of Marine and Environmental Affairs, University of Washington, 3707 Brooklyn Ave NE, Seattle, WA 98105, USA.
[3] Department of Geography, University of Cambridge, Cambridge CB2 3EN, UK.

and their feeding ground distribution serves as an indicator of the resources available in these environments. The unexpected Kermadec Islands migratory bottle-neck of whales from several breeding grounds, variable distribution patterns by life history stage and high pregnancy rates will be important in informing conservation and management planning, and for understanding how this, as well as other whale populations, might respond to emerging threats such as climate change.

1. Introduction

Using animal-borne loggers to monitor the movement and behaviour of wide-ranging predators such as marine mammals, can provide valuable information on the environmental conditions in extreme habitats such as the Southern Ocean (e.g. Aarts et al., 2008; Hindell et al., 2016). Additionally, cross-discipline collaborations can be helpful in identifying patterns in animal movements that are often important when designing conservation strategies (Hays et al., 2016). Therefore, it is increasingly important to collect a suite of data when undertaking field studies in remote sites, or when examining species that are rare, elusive or unable to be caught. Studying migratory animals across their full range poses logistical and operational challenges, particularly for studies of large animals in the complex marine environment (e.g. Heupel et al., 2015). Yet, migration is important for many marine animals, including baleen whales which undertake some of the longest documented annual movements (e.g. Robbins et al., 2011; Stevick et al., 2011), and is therefore an important research area.

The humpback whale (*Megaptera novaeangliae*) requires specific habitats for major life functions: warm waters for breeding and calving, and cold, nutrient-rich waters for feeding. Most humpback populations undertake annual migrations between low-latitude (winter) breeding grounds and high-latitude (summer) feeding grounds (Chittleborough, 1965; Clapham & Mead, 1999; Dawbin, 1966). In the Southern Hemisphere, studying humpbacks within their breeding grounds near continental mainland or islands is logistically attainable. However, within their Antarctic feeding grounds discrete populations of these whales collectively span large areas of open ocean that are largely inaccessible (Amaral et al., 2016).

Commercial whaling heavily exploited all Southern Hemisphere humpback stocks (Clapham & Ivashchenko, 2009; Ivashchenko & Clapham, 2014) and the Oceania whales, that feed in Areas V and VI around Antarctica (Fig. 1) are still estimated to be < 50% of their pre-exploitation numbers. Their recovery is considerably slower than the neighbouring east Australian population and the reasons for this remain unknown (Constantine et al., 2012; International Whaling Commission, 2015). The migratory movements of the Oceania humpback whales as they travel across open-ocean to their remote Southern Ocean feeding grounds are poorly described, and have typically involved single individual movement data. *Discovery* tag data from the 1950s–60s provided the first limited information on the movements of a few individuals, suggesting that these whales likely moved directly north to south between their breeding and feeding grounds (e.g. Chittleborough, 1959; Dawbin, 1964). Later, matches of photo-identified (Robbins et al., 2011) and genotyped individuals (Steel et al., 2018) provided alternate, non-lethal methods of investigating the migratory destinations of this population. However, like *Discovery* tags, these methods provided only endpoint locations, omitting detailed movement information between sampling and resighting locations.

The advancement of satellite telemetry has provided the opportunity to study migratory animals, such as humpback whales, continuously for several months. Telemetry has been an effective tool for
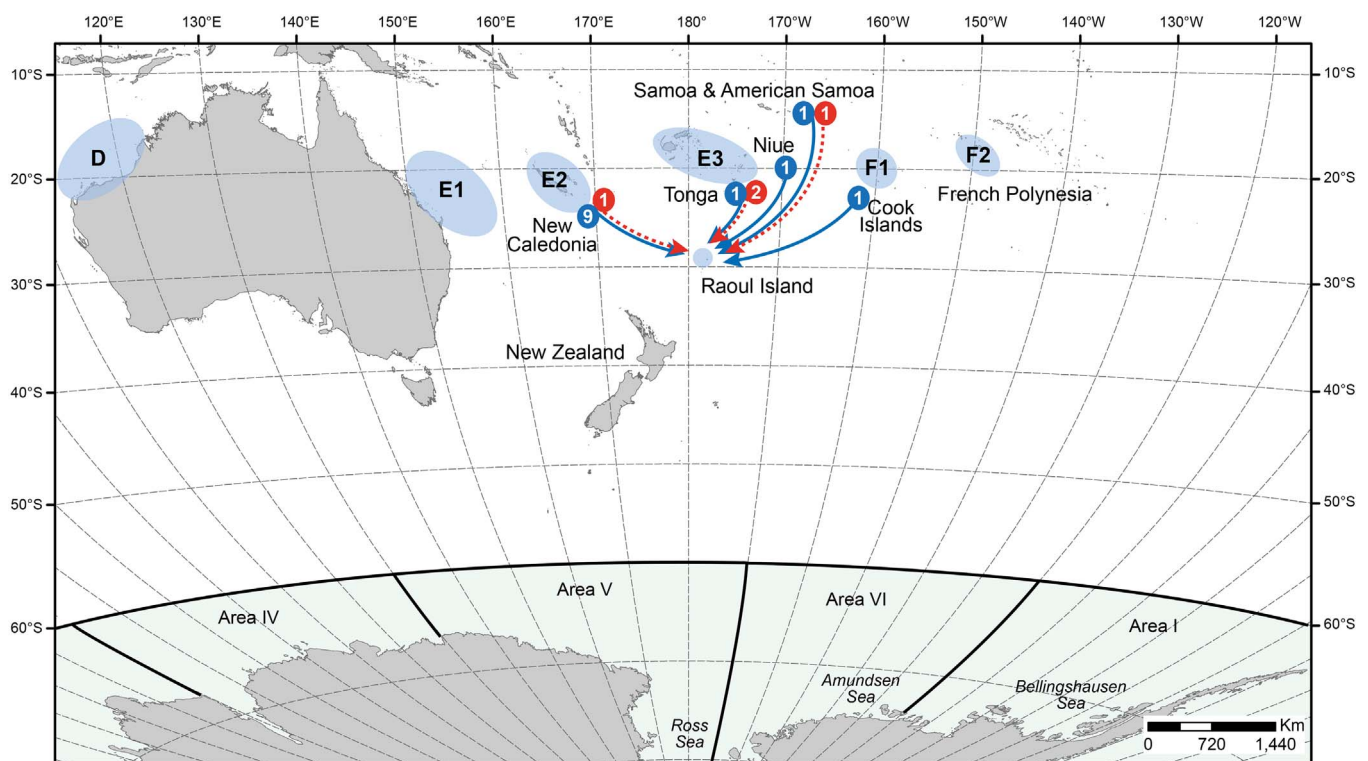

Fig. 1. Breeding (blue areas) and feeding grounds (International Whaling Commission management areas; green areas) of Southern Hemisphere humpback whales. Oceania population comprises breeding grounds E2, E3, F1 and F2. Note that only breeding grounds D-F, and feeding grounds IV, V, VI and I are shown. Arrows denote photo-identification (solid blue) and genotype matches (dashed red) in the current study between various breeding grounds of the Oceania humpback whales and the study site (Raoul Island, Kermadec Islands) in 2015.

describing migration routes and destinations (e.g. Félix & Guzmán, 2014; Garrigue et al., 2010; Zerbini et al., 2006, 2011), behaviour and habitat use patterns (Curtice et al., 2015; Kennedy et al., 2014; Weinstein et al., 2017), and for discovering novel habitats (Garrigue et al., 2015; Zerbini et al., 2006). However, most tag deployments on Oceania humpbacks have occurred on the breeding grounds (Garrigue et al., 2010, 2015; Hauser et al., 2010) and have not been fully integrated with other research tools.

Large whales are challenging to study as they can be difficult to approach and cannot be captured or handled during tag deployment and sample collection. The development of remote biopsy sampling techniques allowed the relatively easy collection of tissue samples from wild cetaceans (Lambertsen, 1987). Now from a small tissue sample (containing skin and blubber) we can obtain information on e.g. the genotype and sex of individuals (Baker et al., 1991; Lambertsen et al., 1988), genetic relatedness (Steeves et al., 2001; LeDuc et al., 2002), age (Jarman et al., 2015; Polanowski et al., 2014), exposure to environmental toxins (Borrell, 1993; Metcalfe et al., 2004), diet (Todd et al., 1997; Clark et al., 2016), and pregnancy status (Kellar et al., 2006; Mansour et al., 2002). The combination of oceanic movement patterns, life history and relatedness markers mean we can integrate several research techniques to answer complex questions about whale populations and their relationship with the Southern Ocean ecosystem.

In this multi-disciplinary study, we combined satellite tagging, genotyping, epigenetic markers, photo-identification and hormone analysis to undertake the most extensive assessment of a highly mobile baleen whale, and of their southern migration to their Antarctic feeding grounds. The movement, behaviour and population demographics of these whales are used as indicators of important habitats within the Southern Ocean ecosystem.

2. Materials and methods

2.1. Data collection

Data were collected off Raoul Island (29°16′S, 177°55′W), Kermadec Islands, New Zealand, from 29th September to 11th October 2015. Land-based observations since 2008 have indicated large numbers of southbound whales passing the Kermadec Islands between mid-September to mid-November (Brown, 2010; Gibson, 2014). We used two rigid-hulled vessels to conduct non-systematic surveys, recording the position, number, and age-class (adults/calves; Clapham et al., 1999) of whale pods. The pods were approached for photo-identification, biopsy sampling, and/or satellite tag deployment; detailed descriptions below.

2.2. Photo-identification

We used digital SLR cameras with 100–400 mm lenses to photograph the ventral surface of whale flukes to identify individuals (Katona et al., 1979). Fluke photographs were quality scored (Friday et al., 2000) and high-quality images were reconciled to create the Kermadec Islands catalogue of whales. The catalogue consisted of 124 photos collected during this study and 12 opportunistic photos from 2007–2015. The images were entered into Fluke Matcher, a computer-assisted matching program (Kniest et al., 2010) and compared to catalogues from the Oceania breeding grounds, the migratory corridors of east Australia, New Zealand and Norfolk Island, and Antarctica (Table A.1; Appendix A in the Supplementary material). Due to the large size of some of the catalogues, this was a preliminary matching effort focusing on the most likely matches; as such, our results do not represent all possible matches.

2.3. Genetics

Biopsy samples were collected using a modified veterinary capture

rifle or a crossbow equipped with 7 × 10 mm or 7 × 20 mm surgical stainless-steel cutting tips. Samples were processed by separating the blubber from the epidermis, with the blubber used for pregnancy assignment. The blubber was frozen at −20 °C, and the epidermis was stored in 70% ethanol. Sloughed skin samples were opportunistically collected from the sea surface.

Total genomic DNA was extracted using standard proteinase K digestion and phenol/chloroform methods (Sambrook et al., 1989), as modified for small samples by Baker et al. (1994). Each sample was used for individual identification and stock analysis by DNA profiling, consisting of sex identification, mitochondrial DNA (mtDNA) control region haplotype (470 bp). Up to fifteen microsatellite loci (EV1, EV14, EV21, EV94, EV96 and EV104; Valsecchi & Amos, 1996; GATA28 and GATA417; Palsbøll et al., 1997; RW18, RW31, RW410 and RW48; Waldick et al., 1999; GT23, GT211 and GT575, Bérubé et al., 2000) were generated following methods previously described by Olavarría et al. (2007) and Constantine et al. (2012).

MtDNA control region sequences were identified to haplotype using Sequencher v4.7 (Genecodes) and all variable sites were visually inspected. Microsatellite alleles were sized with Genemapper v4.0 (Applied Biosystems) and all automated calling was confirmed by visual inspection (Bonin et al., 2004). As a precaution against poor DNA quality, only those samples that amplified at a minimum of 11 microsatellite loci were retained for further analyses (Quality Control dataset). Arlequin v3.1 (Excoffier & Lischer, 2010) was used to test for differentiation in mtDNA haplotype frequency between the Kermadec Islands population, the migratory corridors of east Australia and New Zealand, and the winter breeding grounds in Oceania. The significance of this differentiation was tested with 10,000 random permutations within Arlequin. Replicate genotypes within the Kermadec Islands samples were identified using Cervus v3.0 (Kalinowski et al., 2007). Individuals identified within the Kermadec Islands samples were compared with a curated database of DNA profiles from 2262 humpback whales sampled in three breeding grounds of Oceania (New Caledonia/stock E2, Tonga/stock E3, American Samoa-Samoa-French Polynesia/stock F), two databases from the east Australian migratory corridor (Anderson et al., 2010; Schmitt, et al., 2014a), a database from the New Zealand migratory corridor (Steel et al., 2014), and Antarctic data.

To investigate the origins of whales migrating through the Kermadec Islands we conducted a mixed-stock analysis of mtDNA using SPAM (v.3.7, Alaska Department of Fish and Game, 2003; Debevec et al., 2000). We considered three breeding grounds within Oceania, and the migratory corridor of east Australia as likely source populations and calculated maximum likelihood estimates of contributions from these sources to the Kermadec Islands population using similar methods to Schmitt et al. (2014b). We included the east Australian migratory corridor as a proxy in the absence of breeding ground data. Whales sampled on the Tongan breeding grounds include whales passing the Cook Islands (Garrigue et al., 2011) and are considered a similar stock. The whales of east Oceania (American Samoa, Samoa and French Polynesia) are genetically similar (Albertson et al., 2017) and considered one stock.

2.4. Pregnancy assignment

To assign pregnancy status to sampled whales, progesterone concentrations were quantified from a blubber subsample (Kellar et al., 2006; Mansour et al., 2002). Progesterone was extracted from the blubber using a multitube homogeniser, followed by a series of ethanol, ethanol: acetone, and ethyl ether washes. The resulting lipid residue was separated from the sex-steroid hormones using a biphasic mixture of acetonitrile and hexane. The progesterone concentrations from the steroid pellets were quantified using a progesterone enzyme immunoassay (EIA, ADI-900-011, ENZO Life Sciences). Pregnancy status was assigned for sampled female humpbacks by predicting the probability of being pregnant across a logistic model developed from a series

of humpback progesterone control samples of females of known reproductive status (Pallin, 2017).

2.5. Epigenetic age estimation

We used the Humpback Epigenetic Age Assay (HEAA) method developed by Polanowski et al. (2014) to estimate whale age based on changes in DNA methylation levels at three age-informative CpG sites in three loci: TET2 (ten eleven translocation 2), CDKN2A (cyclin dependent kinase inhibitor 2A), and GRIA2 (glutamate receptor Ia2/AMPA2). Age estimates for whales in our study were based on the calibration used in Polanowski et al. (2014). The overall precision of HEAA (estimated as the standard deviation of the mean difference between known and estimated ages) is 2.991 years, with similar variance throughout the range of ages assayed, although the method generally slightly overestimates the age of young whales and slightly underestimates the age of older whales. Whales with an age estimate of < 2 years (i.e. calves, n = 7) were excluded due to the uncertainty within the method (Polanowski et al., 2014), and as calves could be visually identified in the field by size.

2.6. Satellite tagging and telemetry data analysis

Satellite tags (n = 25) were deployed on adult whales, high on the body near the dorsal fin (Gales et al., 2009) using a modified version of the Air Rocket Transmitter System (Heide-Jørgensen et al., 2001) at 10–12 bar pressure. We used transdermal-implantable, location-only SPOT-5 satellite transmitters (Wildlife Computers, Redmond, USA) housed in stainless-steel cylinders, and sterilised with a chlorhexidine-methylated spirits mixture prior to deployment.

Tags were duty cycled to transmit for 21 h each day to maximise the time with overhead Argos satellites. The maximum number of transmissions per day was set to 600 at a repetition rate of 45 s. Observed locations and estimated errors were calculated by the Argos System when multiple uplinks from a tag were received by a satellite, and raw locations were assigned a location class in a descending order of accuracy: 3, 2, 1, 0, A, B and Z. Location classes A and B have no accuracy estimation and Z is an invalid location.

A hierarchical version of a Bayesian switching state-space model (SSM; Jonsen et al., 2005, 2006) was fitted to the data to estimate locations and behavioural states at a 12-h time-step. We used a SSM as it simultaneously solves for observational and movement models (Jonsen et al., 2005), yielding more accurate estimates of the locations and the associated uncertainty than raw tracking data (Jonsen et al., 2005, 2006). The SSM was fitted in R (R Core Team, 2016) using the software JAGS (Plummer, 2013) and the R packages rjags (Plummer, 2016) and bsam (Jonsen et al., 2015).

Two Markov chain Monte Carlo (MCMC) chains were run in parallel, each for a total of 90000 simulations. The first 50,000 samples were discarded as a 'burn-in', and the remaining samples were thinned, retaining every 50th sample to reduce autocorrelation. The final 1600 independent samples were used to compute the posterior distribution of the model parameter estimates. The behavioural modes (b) were inferred from the means of the MCMC samples, ranging between 1 and 2. We used a conservative approach (Jonsen et al., 2007) for classifying behavioural modes, with mean estimates of $b < 1.25$ labelled as 'transiting', and mean estimates of $b > 1.75$ labelled as 'area restricted search' (ARS), indicative of foraging, resting or breeding behaviour. Locations with a mean b estimate between 1.25 and 1.75 were classified as uncertain in the final dataset.

Total track distance was calculated for each whale as Great Circle distances. Based on visual inspection of tracks and bearings between consecutive locations, the whales began migration at ~ 0030˚S, when the tracks took on a linear south or south-easterly direction. Whales reached the Antarctic feeding grounds (60˚S) when their tracks became more sinuous. The state-space modelled data were used to calculate speeds between consecutive locations for each whale. To determine whether there were differences in travel speed during migration (30–60˚S) and non-migration (< 30˚S, > 60˚S) between females with calves and adults without calves, we conducted a Welch two-sample t-test. The data were log-transformed prior to statistical testing, and results were considered significant at $p \leq 0.05$.

3. Results

3.1. Research effort

Over 13 days we non-systematically surveyed 1480 km around Raoul Island. We encountered 127 pods of humpback whales, containing a cumulative total of 235 adults and 37 calves.

3.2. Photo-identification

A total of 136 individual whales were included in the Kermadec Islands humpback whale catalogue. A total of thirteen individuals were matched to whales from the breeding grounds of New Caledonia (n = 9), Tonga (n = 1), Niue (n = 1), American Samoa (n = 1) and the Cook Islands (n = 1; Fig. 1).

3.3. Biopsy samples and genotype identification

A total of 84 tissue samples were collected (70 biopsy and 14 sloughed skin). Three samples did not amplify due to insufficient quantities of extracted DNA, and one failed to pass Quality Control (QC11) criteria of amplification at a minimum of 11 microsatellite loci. From the remaining 80 samples, we genetically identified 72 individuals (27 males: 45 females).

There were four genotype matches to whales previously sampled on the breeding grounds: New Caledonia (female with a calf; sampled as a calf in 1999), American Samoa (male; 2009 sample), and Tonga (two females; 2003 and 2005 samples; Fig. 1), both were satellite tagged in the current study (PTT112721 and PTT111866). The female matched to New Caledonia was the only whale identified both genetically and photographically.

3.4. Population differentiation and mixed-stock analysis

Review of mtDNA control region sequences identified 33 haplotypes from 71 individuals with confirmed sequence; one individual did not give a clean sequence. The humpbacks migrating past the Kermadec Islands had no 1:1 relationship with any single breeding ground population and were significantly different to all other populations at $p = 0.05$, reflecting the diversity of genotype matches to the Oceania breeding grounds and migratory corridors (Table 1a). We identified one haplotype (EC007, Genbank No. HQ241485) that was previously unknown from the Oceania or east Australia regions. The mixed stock analysis assigned probable breeding ground origins of whales to New Caledonia (49%), Tonga (36%), American Samoa – Samoa – French Polynesia (12%), east Australia (1%) and an unknown stock (2%; Table 1b).

3.5. Pregnancy assignment

Progesterone levels were analysed from 38 blubber samples, including samples from three males and four calves as controls (all classified as not-pregnant). Progesterone levels for one adult female could not be determined. Concentrations, reported as nanograms of progesterone per gram of blubber (ng/g P4), ranged between 1.28 and 5.26 for non-pregnant, and between 25.81 and 352.68 for pregnant individuals (Table B.1; Appendix B in the Supplementary material). Seventeen out of 30 females (56.7%) were classified as pregnant. This included five out of 11 (45.5%) females that were accompanied by a

Table 1

a) Pairwise comparisons for mtDNA haplotype diversity (F_{ST}) between humpback whales sampled at Raoul Island, Kermadec Islands (n = 71 with sequence), the migratory corridors of east Australia and New Zealand, and breeding grounds of Oceania (see Fig. 1). The number in brackets is the number of individuals with sequence used for each population. b) Results of the SPAM mixed stock analysis assigning probability of breeding ground for the humpback whale samples at the Kermadec Islands.

(a)	Sampling site (n)		F_{ST}	p-value
	East Australia (316)	Migratory corridor	0.012	0.000
	New Zealand (151)	Migratory corridor	0.009	0.001
	New Caledonia (953)	Breeding ground	0.004	0.011
	Tonga (337)	Breeding ground	0.005	0.009
	French Polynesia – American Samoa – Samoa (292)	Breeding ground	0.020	0.000

(b)	Population	Estimate	S.E.	C.V
	East Australia	0.0007	0.0031	4.7
	New Caledonia	0.4941	0.1153	0.23
	Tonga	0.3641	0.1444	0.40
	French Polynesia – American Samoa – Samoa	0.1212	0.1006	0.83
	Unknown	0.0200		

calf at the time of sampling, and six out of 11 (54.5%) females, for which we had satellite tag data.

3.6. Epigenetic age estimation

Epigenetic age was estimated for 81 sampled whales, including eight whales sampled twice, and three samples for which age could not be determined (due to poor DNA quality). Thus, 78 age estimates were obtained from 70 individuals to generate an age profile for the sampled population. The mean observed age estimate was 13.8 years (median = 11.6, range = 2.1–67.5, n = 71, excludes whales estimated as < 2 years, Fig. 2).

3.7. Satellite tag deployment

Of 25 tags, six failed to transmit. One tag (PTT131172) transmitted inconsistently for five days, during which the whale never left Raoul Island. Due to insufficient migration data, this tag was excluded from further analyses. The remaining 18 whales comprised 5 females without calves, 6 females with calves, 5 males, and 2 of unknown sex (PTT102211 – no sample, PTT112722 – molecular sex identification unsuccessful). These whales were tracked for an average of 105 days (range = 12–254, Table 2, Fig. 3). Four tags did not transmit for an extended period after deployment (range: 32–66 days), including two that began transmissions after reaching the Antarctic feeding grounds south of 60°S.

3.8. Migratory behaviour and destinations

The average migration duration between the Kermadec Islands (30°S) and the Southern Ocean (60°S) was 51 days (range = 35–67, n = 11). This excluded tags that stopped before 60°S (n = 4), or those for which the first transmission occurred south of 30°S (n = 3). The longest tag transmission duration was 254 days with a total track distance of 13,113 km, including the beginning of the return (northbound) migration (Table 2).

The average speed (± SD) of all whales used for the SSM was significantly different between migration (3.3 ± 1.6 km/h) and non-migration (1.8 ± 1.6 km/h; Welch two-sample t-test, p < 0.01, t = 29.8, 95% CI for difference between means: 0.46–0.53; Table 3). The average speed of females with a dependent calf during migration (3.1 ± 1.5 km/h), and non-migration (1.5 ± 1.4 km/h) was

significantly different from the average speed of adults without calves both during migration (3.4 ± 1.7 km/h), and non-migration (1.8 ± 1.7 km/h; Welch two-sample t-test, p = 0.038, t = 2.0746, 95% CI for difference between means: 0.003–0.100, and p = 0.002, t = 3.14, 95% CI for difference between means: 0.036–0.157, respectively; Table 3).

The SSM tracks show the occurrence of different behavioural states throughout the whales' southern migration (Fig. 4a). The model distinguished between transiting (b < 1.25, 86% of locations) and ARS (b > 1.75, 4% of locations), with the behavioural mode of the remaining 10% of locations categorised as uncertain (1.25 < b < 1.75). The range of b-values varied along the migration path with a general shift towards higher b-values at 60°S (Fig. 4b).

The satellite tracks show that the whales migrated to feeding grounds spanning ~4500 km from eastern Ross Sea to eastern Bellingshausen Sea. Of those individuals whose tags transmitted the entire migration to the feeding grounds, all females with a calf (n = 4) migrated to the Ross Sea region, while 70% of adults without calves (n = 4 females, n = 3 males) migrated to the Amundsen and Bellingshausen Seas. The remaining three adults (one male, two of unknown sex) migrated to the Ross Sea region.

4. Discussion

Obtaining direct measurements to characterise the functioning of a complex system such as the Southern Ocean marine ecosystem can be challenging due to its large size, the complex interactions within the system and the difficulty and cost involved in accessing the region (Girardin et al., 1999). Advances in satellite tracking technology and the miniaturisation of animal-borne loggers have enabled the use of animals as tools to collect information about the ecosystem in remote and inaccessible environments (e.g. Aarts et al. 2008; Hindell et al., 2016). Here we combined multiple research and analytical tools to obtain a comprehensive understanding of the population demography, life history differences and space use of Oceania humpback whales over
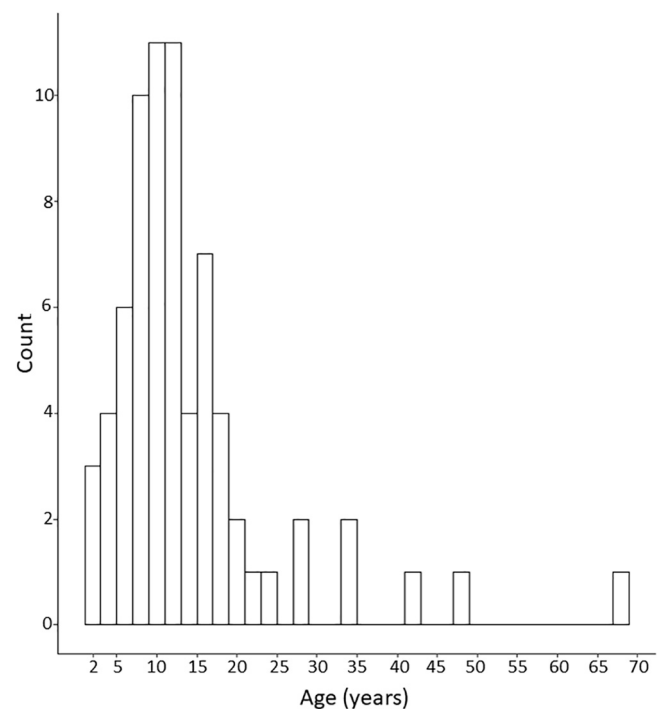

Fig. 2. Population age distribution estimated with the HEAA (Humpback Epigenetic Age Assay) method for n = 71 humpback whale samples collected at Raoul Island, Kermadec Islands in 2015. Ages are grouped into bins of two years. Whales with an age estimate of < 2 years were excluded.
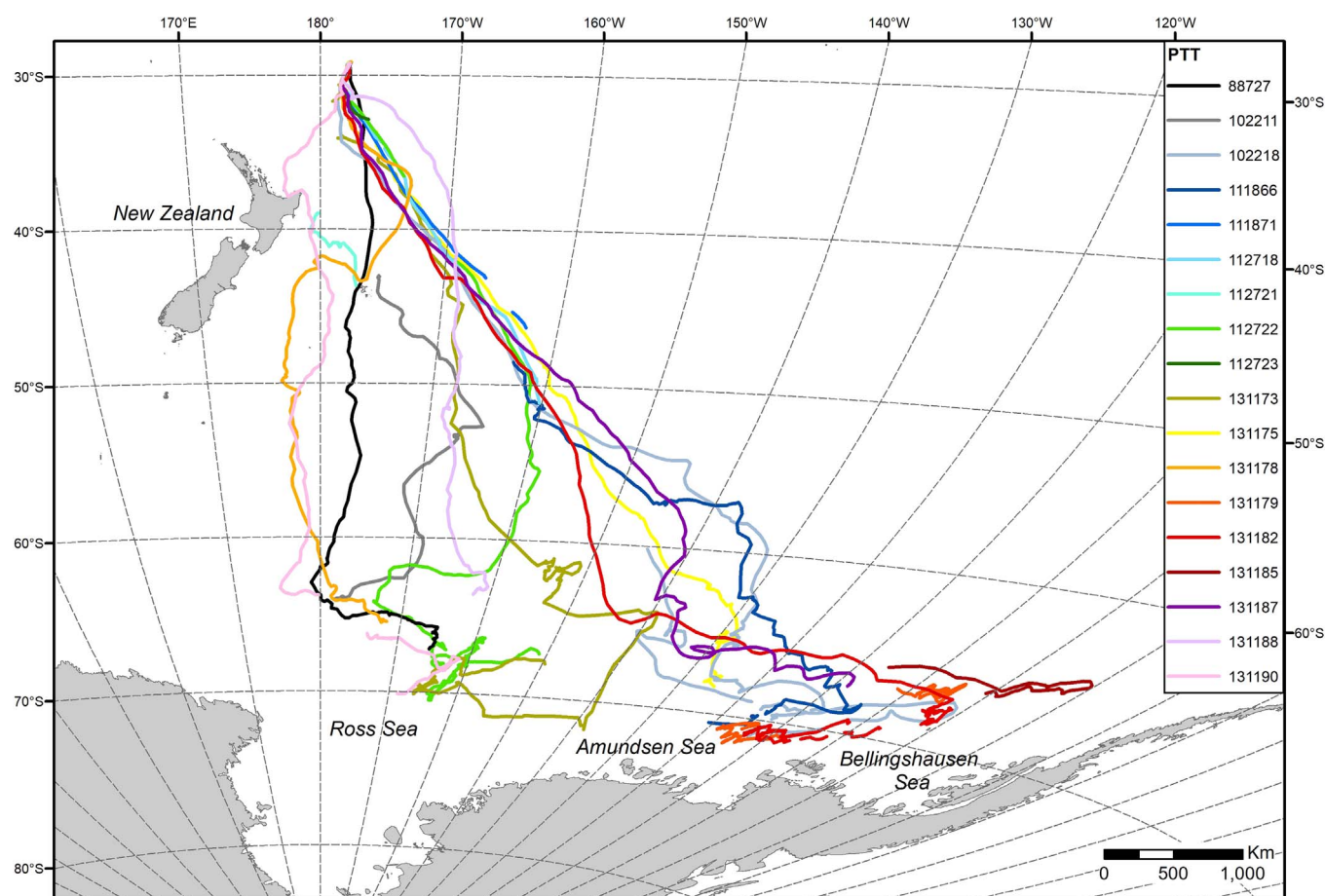
Table 2
Summary of satellite tracking data from 18 humpback whales tagged at Raoul Island, Kermadec Islands in 2015. F = female, M = male, calf refers to a young-of-year animal, and * denotes a pregnant female. Whales of unknown sex: PTT102211 – no sample, PTT112722 – molecular sex identification unsuccessful. All dates are in UTC. Tracking duration = from first to last transmission. Data days = number of days when one or more locations were received. Track distance is calculated using state-space modelled data.

Tag PTT number	Sex – behaviour class	Deployment date	First transmission	Last transmission	Tracking duration (d)	Data days (d)	Track distance (km)
88,727	F + calf	08 Oct 15	08 Oct 15	14 Jan 16	99	99	5369
102,211	Unknown	10 Oct 15	11 Oct 15	19 Dec 15	70	57	5124
102,218	M	10 Oct 15	11 Oct 15	20 Jun 16	254	249	13,113
111,866	F*	04 Oct 15	06 Nov 15	15 Mar 16	131	130	5877
111,871	F	08 Oct 15	09 Oct 15	04 Nov 15	27	26	2359
112,718	M	05 Oct 15	05 Oct 15	13 Nov 15	40	40	3234
112,721	F + calf	09 Oct 15	10 Nov 15	28 Nov 15	19	19	752
112,722	Unknown	10 Oct 15	11 Oct 15	03 Apr 16	176	174	8307
112,723	F* + calf	06 Oct 15	07 Oct 15	18 Oct 15	12	12	500
131,173	M	30 Sep 15	30 Sep 15	08 Apr 16	192	184	10,174
131,175	M	04 Oct 15	04 Oct 15	18 Jan 16	107	97	6395
131,178	F* + calf	08 Oct 15	09 Oct 15	17 Jan 16	101	101	5524
131,179	M	02 Oct 15	07 Dec 15	22 Mar 16	107	84	2844
131,182	F*	01 Oct 15	02 Oct 15	02 Apr 16	184	150	10,497
131,185	F*	02 Oct 15	27 Nov 15	06 Jan 16	41	41	1900
131,187	F	30 Sep 15	01 Oct 15	02 Jan 16	94	94	7303
131,188	F* + calf	29 Sep 15	30 Sep 15	11 Dec 15	73	73	4749
131,190	F + calf	08 Oct 15	08 Oct 15	20 Mar 16	165	90	6755

their large spatial range. We reveal a young population of whales indicating recovery from exploitation, from winter breeding grounds spanning ~3500 km, with high pregnancy rates not reflected in the rate of population recovery. The whales had different migratory trajectories depending on their reproductive state and spread across ~4500 km of Antarctic waters to feed during the productive summer months.

4.1. Differential dispersal to feeding grounds

Our findings suggest that Oceania humpback whales may migrate to different feeding grounds based on their life history stage. All tagged females with calves tracked through their full migration travelled to the Ross Sea region, whereas most adults without calves travelled east to the Bellingshausen Sea. This pattern, whereby the presence of a calf may influence the choice of feeding ground destination for female

Fig. 3. State-space model derived tracks for 18 humpback whales satellite tagged at Raoul Island, Kermadec Islands in 2015.

Table 3

Average and median (± SD) travel speeds (km/h) for humpback whale adults without (w/o) calves and females with (w/) a young-of-year calf during migration (30–60°S), and non-migratory (< 30°S, > 60°S) phases. The number of individual whales and the number of data points used to calculate speeds and conduct t-tests are shown. Calculations were done using state-space modelled data from the tags of 18 whales (note that some tags only transmitted during the migration, or non-migration phase).

	During migration				Non-migration			
	Average	Median	SD	Individuals (data points)	Average	Median	SD	Individuals (data points)
Adult w/o calf	3.4	3.5	1.71	10 (889)	1.8	1.2	1.66	12 (1730)
Female w/calf	3.1	3.1	1.48	6 (452)	1.5	0.9	1.44	5 (323)
All whales	3.3	3.3	1.64	16 (1341)	1.8	1.2	1.63	17 (2053)

humpbacks, was also reflected in a historical whaling catch data (Appendix C in the Supplementary material).

Differential habitat use occurs in some mammals and may be a result of differences in energetic requirements, environmental conditions, social mechanisms or risk of predation (e.g. Loe et al., 2006; Main et al., 1996). Humpback whales exhibit some age- and sex-linked differences, most notably the staggered time of departure and arrival at breeding and feeding grounds (Chittleborough, 1965; Dawbin, 1966, 1997). Also, small-scale habitat use patterns vary on the breeding grounds depending on sex and reproductive status (Craig & Herman, 2000; Lindsay et al., 2016; Smultea, 1994). However, the large-scale division based upon reproductive status that we observed in this study has not, to our knowledge, been reported across feeding grounds. Although differences in the spatial distribution of some sex or age classes have been observed within feeding grounds such as the Gulf of Maine in the North Atlantic (Clapham & Mayo, 1987; Robbins, 2007), our study is on a much larger scale (distances of 2000 km + vs ~ 400 km).

Humpbacks have been found to show natal fidelity to feeding grounds, where the calf learns the migration path from their mother during the first year of life (e.g. Acevedo et al., 2006; Baker et al., 1990, 2013; Clapham & Mayo, 1987). Our findings however suggest a possible deviation from the traditional view of maternally inherited migration routes and feeding ground destinations. Calves may migrate to the Ross Sea during their first year, and to either the Ross Sea or the Amundsen and Bellingshausen Seas later in life. The utilisation of the region north of the Ross Sea for feeding, especially by females with dependent calves, may be used as an indicator of the ecological resources available in the marine environment, and highlights the conservation importance of this area.

Our satellite tracking shows several adult humpback whales migrating towards the broader Amundsen and Bellingshausen Sea area, which has remained poorly studied (e.g. Kaiser et al., 2009; Griffiths, 2010; Munilla & Soler-Membrives, 2015). Humpback whales have huge energetic demand and their presence in the Amundsen and Bellingshausen Seas region could be taken as an indicator of the quality and suitability of this habitat to satisfy their energetic needs. This region must be able to support sufficient amounts of krill (Euphausia superba), the whales' main prey, to provision for the (slowly) recovering whale population. Comparisons with future tracking studies of these whales' distribution will be informative in assessing changes in prey availability in this region.

It is worth noting how in our case, the additional information on the reproductive status of the animals was key to interpreting the distribution data. Knowledge of the reproductive status of individuals using different regions for feeding could be relevant in the future when examining fluctuations in their distribution patterns, as one reproductive class might respond more strongly to changes in the environment or prey availability. Future research should now aim to validate these findings of different migratory destinations in the Oceania population and distinguish whether such division is due to life history related requirements, differences in productivity between feeding habitats or the energetic cost associated with migration distance. Within the Southern Ocean, this dispersal pattern could result in different exposure to threats (e.g. fisheries, climate change effects) by life history

stage, with potentially complex implications for the management and conservation of this population.

4.2. Migration behaviour

Baleen whales undertake some of the longest migrations known, and the Kermadec Islands humpbacks crossed ~ 50° of latitude, and ~ 110° of longitude, one way, between their breeding and feeding grounds. The straight-line distances from breeding grounds (with photo-identification or genetic matches) to Kermadec Islands ranged from ~ 900 km (Tonga) to ~ 2000 km (Cook Islands), and from Kermadec Islands to the Antarctic feeding grounds from ~ 4500 km (Ross Sea) to ~ 6000 km (Amundsen and Bellingshausen Seas). Reported extreme long-distance movements (> 7000 km) between feeding and breeding grounds (Rasmussen et al., 2007; Robbins et al., 2011; Stevick et al., 1999, 2011; Stone et al., 1990) have mainly involved a single or a few individuals and were generally considered exceptional. Our simultaneous tracking of several individuals highlights that long-distance migration from Oceania to the Amundsen and Bellingshausen Seas region is not exceptional, and confirms previous single records (Hauser et al., 2010; Robbins et al., 2011). The energetic costs of the different migration distances (Ross Sea vs Amundsen and Bellingshausen Seas), the effects on the fitness and reproductive potential of individuals of different life history stages, and the consequences of climate change on krill availability in these areas should be investigated.

The travel speeds we report are comparable to previous studies (Garrigue et al., 2015; Kennedy et al., 2014; Lagerquist et al., 2008; Rosenbaum et al., 2014). Females with calves were slower than other adults, however, due to a large sample size this difference, while statistically significant, may not be biologically meaningful. Other baleen whales have been shown to have similar speed differences: for example, North Atlantic right whale (Eubalaena glacialis) females with calves were slower than adults without calves (Hain et al., 2013). Andriolo et al. (2014) tagged pairs of humpbacks within larger groups, and a mother-calf pair was found to move slower than the adult female associated with them when they were tagged. Within the Oceania population, slower travel speeds by mother-calf pairs could be linked to the feeding ground destination. Females with calves could be theorised to migrate to the Ross Sea as this is a shorter and more direct route to the feeding grounds from Kermadec Islands, with possibly a lower energetic cost for the young calf or the lactating mother.

The SSM identified different behavioural modes in the data, with the high number of transiting points reflecting the long migration. The shift in whale behaviour at ~ 60°S, at which point the whales began to move more sinuously, presumably in search of prey, roughly coincided with the locations of the Antarctic Circumpolar Current (ACC) fronts (the placement of which fluctuate from year-to-year; Kim & Orsi, 2014). Some of the fronts of the ACC have been associated with productivity (e.g. Tynan, 1998; Bost et al., 2009). The change in whale behaviour may therefore be due to the whales encountering productive conditions and possibly the first patches of krill. Future northward or southward movement in the shift from migratory behaviour to feeding could serve as an indicator of changes in krill availability and distribution.

Humpback whales occasionally feed outside Antarctic waters and
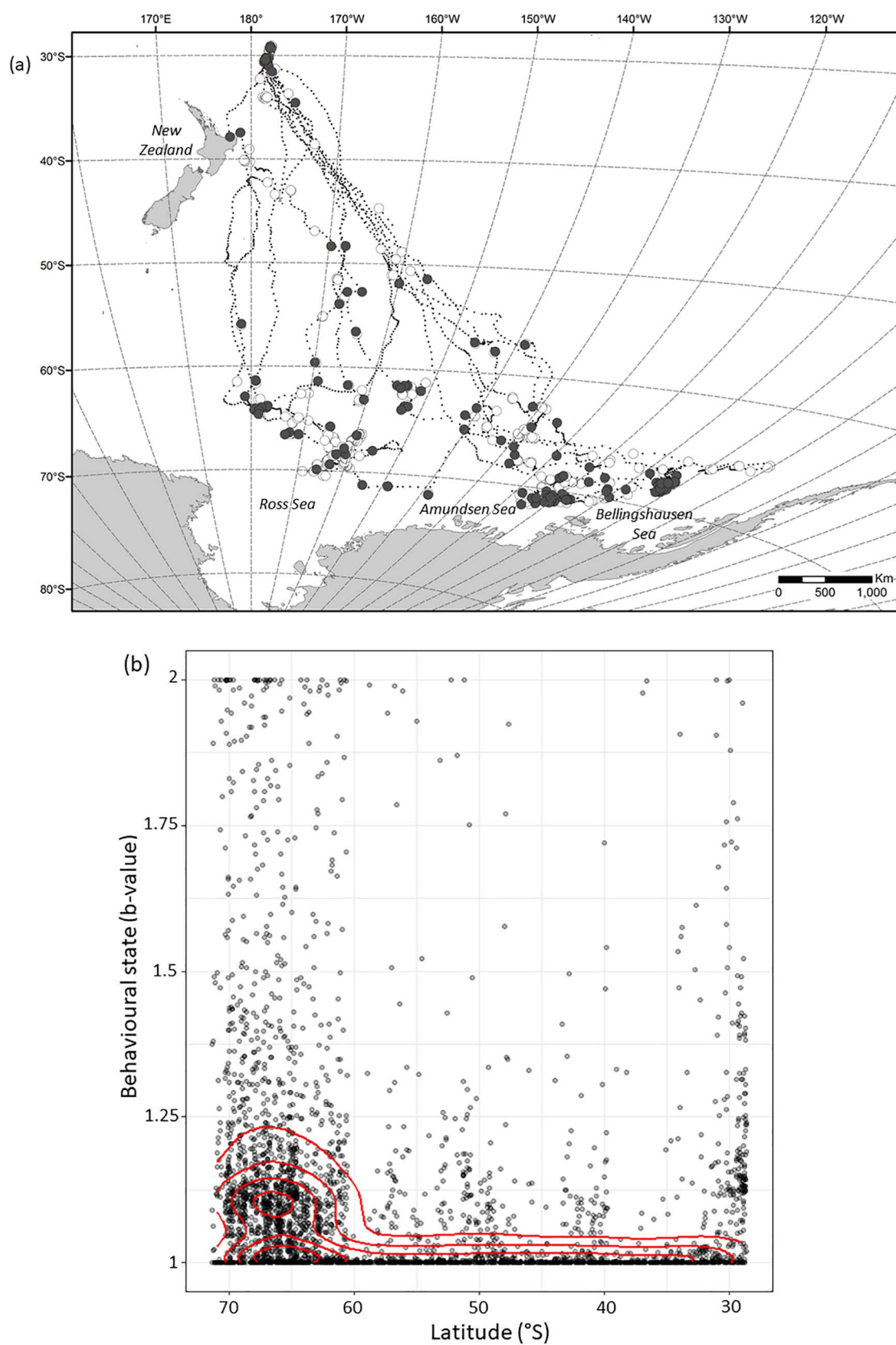
Fig. 4. a) State-space modelled tracks of 18 humpback whales showing behavioural states identified by the model at each location (dot = transit, open circle = uncertain, filled in circle = area restricted search, and b) distribution of b-values (denotes behavioural state) from the state-space model by latitude (b < 1.25 = transit, 1.25 < b < 1.75 = uncertain, b > 1.75 = area-restricted search). Red line represents a 2D density plot (kernel density estimation) of the data.

during their southern migration, e.g. off south-eastern Australia (Owen et al., 2015; Stamation et al., 2007; Stockin & Burgess, 2005), and possibly off south-western New Zealand (Gales et al., 2009). In some areas this may be important in the annual energy budget. In our study, nine whales exhibited ARS behaviour outside the feeding grounds, accounting for 1.7% of all modelled locations during migration. This ARS behaviour may have been opportunistic feeding, or a collection of behaviours that have similar movement characteristics (e.g. resting, socialising, mating). Future studies should quantify the role of supplementary feeding for the Oceania humpbacks that will allow comparisons with the rapidly increasing east Australian whales. Additionally, increase in the feeding activity during migration might serve as an indicator of the Southern Ocean ecosystem in that the energetic requirements of the whales aren't fully met during the summer feeding season.

4.3. Age distribution and pregnancy

The age profile of whales migrating past the Kermadec Islands is an indicator of a recovering Oceania population. With an average age of 14 years the profile was similar to an epigenetic-based estimate of the adjacent east Australian population (Polanowski et al., 2014). Both populations had a high proportion of younger individuals and a relatively low proportion of older individuals. Comparison of the east Australian age estimates with the population's expected pre-exploitation age structure was suggestive of high fecundity in the population (Polanowski et al., 2014). Given the adjacency of the areas, we assume that the pre-exploitation age structure for Oceania humpbacks was comparable. Determining population age structure can be a powerful tool for ascertaining the impact of exploitation on populations of long lived animals (Jones et al., 2018).

Over half (57%) of all sampled females were pregnant. This is similar to earlier studies (Baker et al., 1987; Chittleborough, 1965; Clark et al., 2016), and to a recent estimate of 58% from the Western Antarctic Peninsula (Pallin, 2017). However, our findings may not be representative of the population. Although the field work was conducted at the peak of the southern migration past the Kermadec Islands, and we aimed to sample all possible whales, there is a chance of bias. Humpbacks stagger their departure from their breeding grounds by life history stage (Chittleborough, 1965; Dawbin, 1966, 1997). Due to a short sampling period at the Kermadec Islands, we may have captured uneven proportions of these migration cohorts. Additionally, we do not have an accurate estimate of the proportion of sampled females that were not sexually mature at the time of sampling. The average age at sexual maturity in humpback whales is known to range from ~5 to 10 years (Chittleborough, 1965; Clapham, 1992; Gabriele et al., 2007; Zerbini et al., 2010), and although likely to be similar, this has not been estimated for the Oceania population.

Almost half of the females with new-born calves were also pregnant, suggesting a higher rate of annual pregnancies than expected. Female humpbacks generally have an inter-calf interval of ~2–3 years (e.g. Chittleborough, 1958, 1965; Clapham & Mayo, 1990; Gabriele et al., 2017), with annual pregnancies less common (e.g. Barlow & Clapham 1997; Clapham and Mayo, 1990; Glockner-Ferrari & Ferrari, 1990; Robbins, 2007). However, most of the information has come from Northern Hemisphere whales. Recent work in New Caledonia has estimated a 1.4-year inter-calf interval (Chero, 2017).

The high pregnancy rates observed in the Oceania population is in contrast to the estimated low population size and relatively slow recovery rate (Constantine et al., 2012; IWC, 2015). This discrepancy could be due to calf loss, possibly in the form of foetal resorption, or early termination of pregnancy that can occur in mammals in response to changing environmental conditions or stressors (e.g. Conaway et al., 1960; Huck et al., 1988). The sampling for our study occurred soon (~6–8 weeks) after the peak of the breeding season (Chittleborough, 1958, 1965; Garrigue et al., 2001) and the whales may not have experienced conditions resulting in foetal loss. However, similar rates of pregnant females (58%) and annual pregnancies (52%) were reported from the Western Antarctic Peninsula ~5–8 months into the 12-month gestation period (Pallin, 2017). We currently do not have an estimate of foetal and neonatal mortality for the Oceania population, nor of the recruitment rate of calves into the population. Such inference would require resightings of previously sampled females to ascertain the fate of the pregnancy.

The high pregnancy rate could indicate that the foraging areas are able to support a high proportion of females with increased energetic need due to gestation. Future monitoring of the pregnancy rates could serve as an indicator of the energetic gain females obtain during the summer feeding season.

5. Conclusions

Here we show how combining new techniques and different analysis methods can be an efficient approach for investigating a key ecological species, and its environment, that may otherwise be hard to access. For the Oceania humpback whale population, this work represents the most comprehensive study on the population demography, life history differences and space use patterns over their large spatial range. The life history stage of the whales may have influenced their choice of two Antarctic feeding regions. This is important when informing conservation and management planning as whales may be exposed to very different climate change and anthropogenic pressures. This highlights the need for sufficient knowledge of the dispersal patterns and population demography for understanding how individuals and populations respond to future environmental change. Sampling and satellite tagging whales further north, closer to their breeding grounds, was a cost-effective alternative to expensive and logistically difficult voyages to the remote Southern Ocean. Comparisons with future re-sampling and satellite tagging could provide valuable insight into changes in the distribution of the whales' main prey (krill) as well as into possible factors affecting the whales' future recovery.

Data accessibility

Data will be deposited in the GenBank and Figshare public data repositories following acceptance of the manuscript.

Declarations of interest

None.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2018.02.030.

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